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CONCEPT PAPER

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Phylogenetic scale in ecology and evolution

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Abstract

Aim: Many important patterns and processes vary across the phylogeny and depend on phylogenetic scale. Nonetheless, phylogenetic scale has never been formally conceptualized, and its potential remains largely unexplored. Here, we formalize the concept of phylogenetic scale, review how phylogenetic scale has been considered across multiple fields and provide practical guidelines for the use of phylogenetic scale to address a range of biological questions.

Innovation: We summarize how phylogenetic scale has been treated in macroevolution, community ecology, biogeography and macroecology, illustrating how it can inform, and possibly resolve, some of the longstanding controversies in these fields. To promote the concept empirically, we define phylogenetic grain and extent, scale dependence, scaling and the domains of phylogenetic scale. We illustrate how existing phylogenetic data and statistical tools can be used to investigate the effects of scale on a variety of well-known patterns and processes, including diversification rates, community structure, niche conservatism or species-abundance distributions.

Main conclusions: Explicit consideration of phylogenetic scale can provide new and more complete insight into many longstanding questions across multiple fields (macroevolution, community ecology, biogeography and macroecology). Building on the existing resources and isolated efforts across fields, future research centred on phylogenetic scale might enrich our understanding of the processes that together, but over different scales, shape the diversity of life.

KEYWORDS
biodiversity, community structure, conservation, diversification, domains of scale, genetics, genomics, microbiology, spatial scale

1 | INTRODUCTION

Numerous patterns in ecology and evolution vary across the phylogeny. Species richness declines with latitude across orders and classes, but not necessarily across their constituent genera (Buckley et al., 2010; Marquet, Fernández, Navarrete, & Valdovinos, 2004). Phylogenetic delimitation of species pools influences our inferences about the processes that form local communities (Cavender-Bares, Kozak, Fine, & Kembel, 2009; Chalmandrier et al., 2013). Many other examples also illustrate that patterns in ecology and evolution might depend on phylogenetic scale (Figure 1). Nonetheless, unlike the extensively developed concepts of spatial and temporal scale, where scale dependence in the patterns and processes has long been acknowledged (Chave, 2013; Levin, 1992; Wiens, 1989; Willis & Whittaker, 2002), the importance of phylogenetic scale has only recently begun to be recognized. Here, we formalize and develop the concept of phylogenetic scale, summarize how it has been considered across fields, provide empirical guidelines for the treatment of phylogenetic scale and suggest further research directions.

Phylogenies represent a hierarchy of mutually nested clades whose position relative to each other can be used to define phylogenetic scale. Phylogenetic scale can be measured in various ways (taxonomic ranks, clade age, clade size or other measures; Box 1) and, in some cases, we can distinguish further between phylogenetic extent and phylogenetic grain (Figure 2a–c and Box 1). In community ecology, for example, analyses based on

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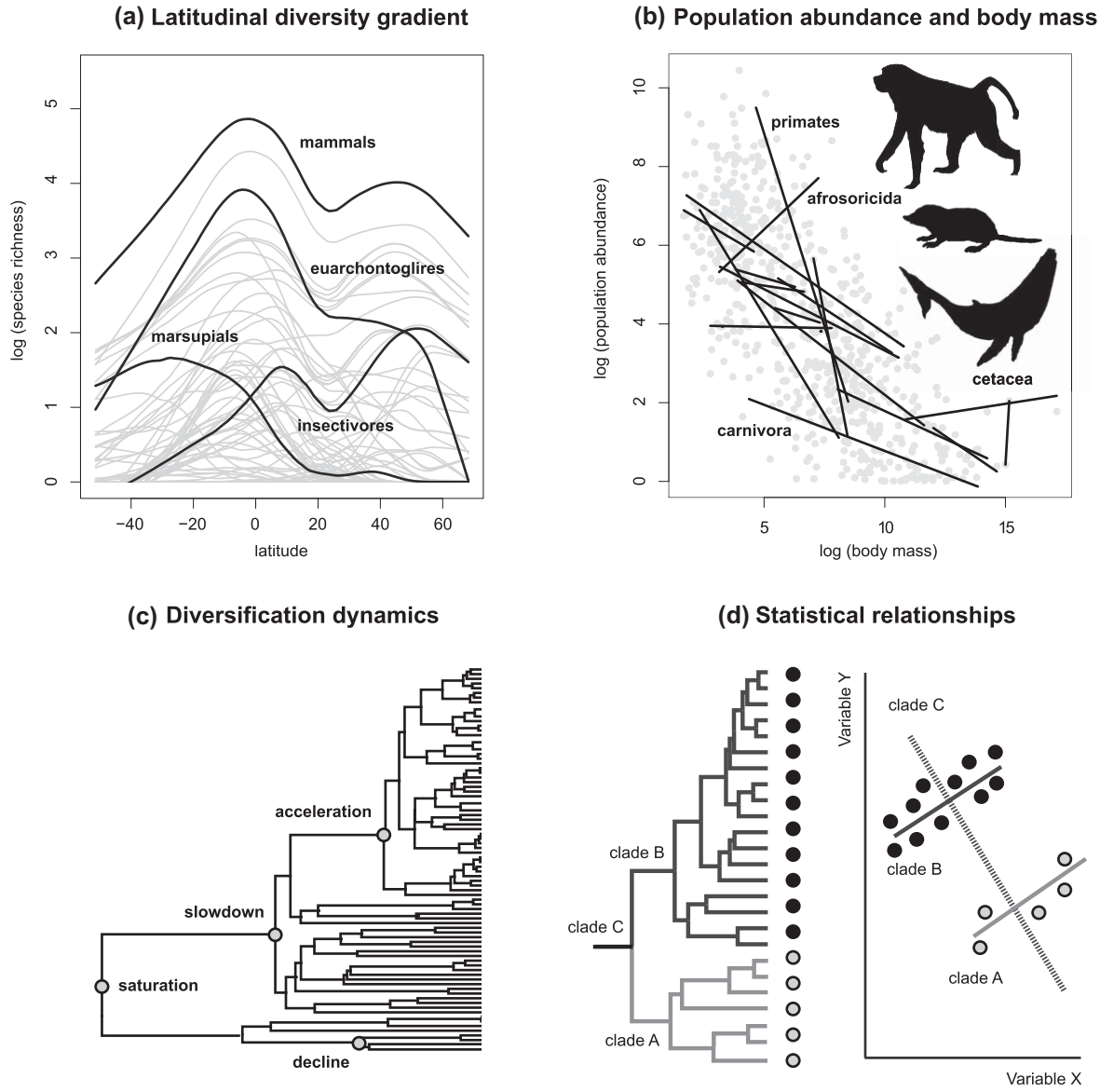

FIGURE 1 Examples of patterns that vary across phylogenetic scales. (a) The latitudinal diversity gradient. Mammal diversity decreases with latitude across large clades, but many other patterns emerge across small clades, including inverse ones (select clades depicted in black). (b) The dependence of population abundance on body mass. The dependence is negative across large phylogenetic scales (mammals depicted in grey) but varies substantially across small scales (select clades depicted in black). (c) Diversification dynamics. Expansionary dynamics detected at some scales are not in conflict with saturation taking place at other scales. (d) Statistical correlations. Even though the depicted variables are positively correlated within each of the two subclades, the correlation becomes negative when the subclades are studied together. The data were taken from the IUCN (IUCN, 2017) and PanTHERIA (Jones et al., 2009)

large phylogenetic extents, such as angiosperms, typically suggest that community composition has been shaped by environmental filters, whereas analyses of small extents (e.g., white oaks) often implicate a suite of additional mechanisms (such as competition, mutualisms and dispersal limitation; Cavender-Bares et al., 2009). By examining multiple grains (clades of different ages) within a given phylogenetic extent (families of birds), researchers found that old clades show higher sympatry than young clades, as expected under the model of allopatric speciation followed by secondary sympatry (Barraclough & Vogler, 2000). Sometimes, however, it might be preferable to investigate patterns and processes with respect to phylogenetic scale without making the distinction between grain and extent (Figure 2d and Box 1).

Despite the massive increase in phylogeny-based research over the last years (O'Meara, 2012), studies that systematically investigate how patterns and processes change with phylogenetic scale (e.g., niche conservatism, community structure, diversification rate) or use phylogenetic scale to identify the 'laws of ecology' [i.e., universal patterns that hold across scales, such as species-abundance distributions (SAD) or latitudinal gradients] are still relatively scarce. Consequently, it seems likely that the full potential of the growing body of the

Box 1. The concept of phylogenetic scale

The concept of scale is based on the fact that some entities (e.g., regions, clades) can be ordered relative to one another into a hierarchy. The relative position within the hierarchy (i.e., above, below) then defines scale (*scala* means ladder in Latin). For example, continents contain biomes, ecoregions and localities, giving rise to a spatial hierarchy that defines spatial scale (Wiens, 1989). Likewise, large clades contain small clades, producing a hierarchy that can be used to define phylogenetic scale.

Phylogenetic scale is precisely defined for nested clades, which can be easily ordered relative to one another. However, in many cases, we need to define phylogenetic scale for non-nested clades, whose ordering is less intuitive and requires some standardized measures. Taxonomic ranks have traditionally served as one such measure, but ranks for distantly related taxa are rarely comparable (e.g., genera in mammals and genera in insects). Alternatives include clade age, clade size, node-to-root distance, tree depth (i.e., time slices through the tree) or the degree of molecular and phenotypic divergence (measured on a phylogram as the total number of nucleotide substitutions, derived characters, etc., within a clade). Even these measures are not comparable in all circumstances (e.g., clades of a similar size might not be comparable in terms of their phenotypic divergence), but the same applies to the measures of spatial scale. Spatial grains of standardized sizes, for example, might not ensure comparability across species with dramatically different home range sizes (Levin, 1992). This means that there is not a single all-purpose measure for phylogenetic scale. Instead, the most suitable measure should be chosen based on the biological properties of the system (e.g., body size, generation time, rates of morphological evolution) and the attribute we wish to evaluate (e.g., diversification rate, the strength of trait conservatism, regression slope between two variables).

Once the attribute of interest and the most appropriate measure of phylogenetic scale are identified, we can study the attribute specifically with respect to the scale axis (*sensu* Figure 2d). For example, niche conservatism might decline with clade age, whereas the strength of diversification slowdowns might increase with clade size. This type of research can generate fundamental insights, as amply evidenced by previous work on spatial scale. The species–area relationship (SAR), for example, describes changes in species richness with respect to a measure of spatial scale (i.e., geographical area), producing a variety of key insights for biodiversity theory, conservation and management (Chave, 2013; Storch, 2016).

In some cases, it is illuminating to distinguish between phylogenetic grain and extent. In spatial scale, grain refers to the area of the elementary unit of analysis (e.g., grid cells within a continent), whereas extent refers to the total area analysed (e.g., the continent). Likewise, phylogenetic grain refers to the elementary unit of analysis (defined in terms of clade age, clade size, or, perhaps less exactly, taxonomic rank), whereas phylogenetic extent refers to the total phylogeny that would encompass all the elementary units analysed. For example, environmental seasonality and the strength of niche conservatism can be calculated for multiple genera (phylogenetic grain) within birds (phylogenetic extent) and correlated with each other. We can investigate the changes in the correlation coefficient with respect to changes in the phylogenetic grain (e.g., genera, families, orders, within birds) and/or changes in the phylogenetic extent (e.g., genera across birds, tetrapods, vertebrates) of the analysis (Figure 2a–c). In community phylogenetics, metrics that capture different grains of the phylogenetic structure of a community can be explored against the background of various phylogenetic extents (see section 2.2 Community ecology). Note that phylogenetic grain cannot be defined separately from phylogenetic extent, and vice versa. Moreover, the distinction between grain and extent applies to the analysis (e.g., correlation analysis, regression analysis), rather than to the attributes analysed (e.g., niche conservatism).

Even though phylogenetic scale might sometimes be approximated conveniently using temporal scale (clade age, time slices through the tree, etc.), the two types of scale are principally different (Jablonski, 2007). Temporal scale ignores phylogenetic hierarchy and, in many cases, fails to capture the patterns across the phylogeny adequately. For example, a phenotypic trait might evolve at different rates across closely related clades (e.g., because of clade-specific selection regimes), such that the same temporal scale becomes associated with very different degrees of phenotypic divergence. In this case, the degree of phenotypic divergence might serve as a more suitable (time-independent) measure of phylogenetic scale, which delimits clades comparable in terms of their phenotypic evolution.

phylogenetic data and that of the methods being continuously developed to analyse them have not yet been realized. We contend that this combination of factors makes the concept of phylogenetic scale particularly timely. More rigorous treatment of phylogenetic scale might produce a more in-depth understanding of biological patterns and processes, similar to that previously produced by the explicit consideration of temporal and spatial scale (Chave, 2013; Levin, 1992; Wiens, 1989; Willis & Whittaker, 2002). We hope that our work will inspire further debate, provide the common ground for cross-field discussion and advance the notion of phylogenetic scale in ecology and evolution.

2 | PHYLOGENETIC SCALE IN CURRENT RESEARCH

Different fields in ecology and evolution have considered the concept of phylogenetic scale to varying degrees, from acknowledging that patterns change across scales to explicit scale-based analyses. The fields often

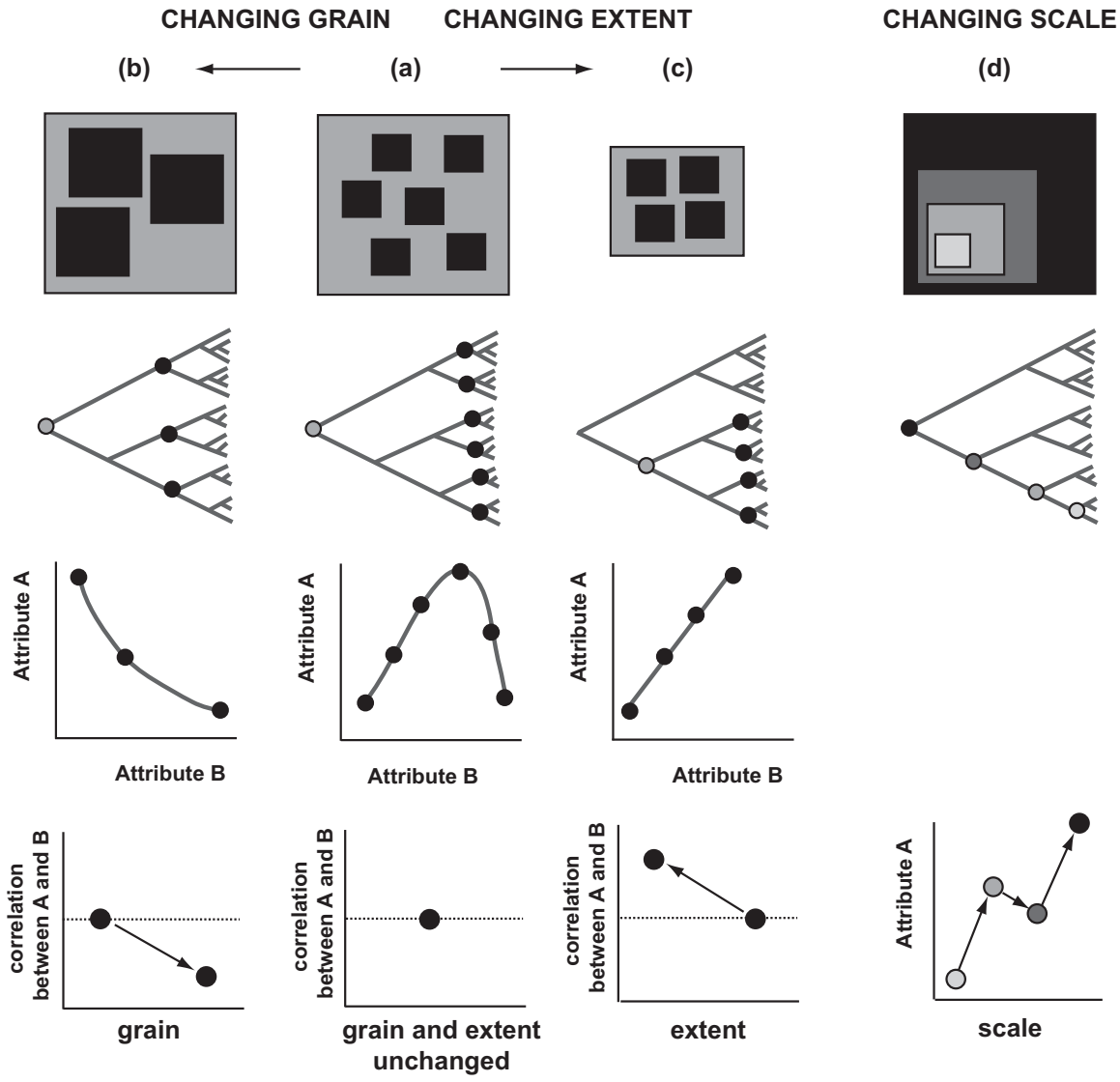

FIGURE 2 Investigating patterns across grains, extents and scales. The first row illustrates changes in spatial grain (from a to b), changes in spatial extent (from a to c) and changes in spatial scale (d). Likewise, the second row illustrates changes in phylogenetic grain (from a to b), changes in phylogenetic extent (from a to c) and changes in phylogenetic scale (d). We can investigate an attribute of interest directly with respect to the scale axis (bottom row of panel d) or we can correlate the attribute with another one (third row), and study their correlation with respect to changing the grain (bottom row of panel b) and changing the extent of the analysis (bottom row of panel c). In the depicted example, increasing the grain changes the unimodal relationship ($r = 0$) to a negative correlation ($r < 0$), whereas decreasing the extent produces a positive correlation ($r > 0$). The phylogeny used to define phylogenetic scale can be a cladogram (branch lengths are not needed to define phylogenetic scale if the analysed clades are nested), phenogram (branch lengths reflect the number of nucleotide substitutions, derived characters, etc.) or chronogram (time-calibrated branch lengths)

differ in how they measure phylogenetic scale (e.g., clade size, clade age, taxonomic ranks) and explore patterns across scales (e.g., varying the grain or the extent of the analysis, or simply studying how an attribute changes across scales). In this section, we describe current research on phylogenetic scale and illustrate how different fields might benefit from the concept, common vocabulary and shared methodology that might lay the foundations for further cross-field discussion.

2.1 | Evolution and diversification

Evolutionary diversification (net outcome of speciation and extinction) and disparification (divergence of trait values within a clade) are known to vary across phylogenetic scales. Even though there is a suite of methods to explore diversification and disparification across a phylogeny (Alfaro et al., 2009; Ingram & Mahler, 2013; O'Meara, 2012; Rabosky, 2014; Tables 1 and 2), most studies report macroevolutionary patterns without investigating them specifically with respect to phylogenetic scale. Such investigation seems increasingly important, as large phylogenies (≥1,000 species), comprising increasingly heterogeneous patterns, are now routinely analysed (O'Meara, 2012). By investigating the patterns across phylogenetic grains, extents and scales (Figure 2), we might start to resolve some of the outstanding controversies in the field.

One such controversy revolves around the dynamics of diversity and diversification. It has been debated whether the dynamics are

expansionary, such that regional and clade diversity accumulate constantly over time (Benton & Emerson, 2007; Harmon & Harrison, 2015; Nee, Mooers, & Harvey, 1992) or whether the dynamics are ecologically limited, such that diversity tends toward an equilibrium (Jablonski & Sepkoski, 1996; Rabosky & Hurlbert, 2015; Rabosky & Lovette, 2008). Genera with dozens of species show a variety of dynamics, including expansion (Benton & Emerson, 2007; Harmon & Harrison, 2015; Wiens, 2011) and decline (Morlon, Parsons, & Plotkin, 2011). In contrast, higher taxa with thousands of species are often saturated at their equilibrium diversity (Rabosky & Hurlbert, 2015); although cases of expansion in very large clades have also been reported (e.g., birds, tetrapods; Hedges, Marin, Suleski, Paymer, & Kumar, 2015; Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). Moreover, changes in diversification rates from lower to higher taxa are well documented in the fossil record and island radiations (Benton & Emerson, 2007; Glor, 2010). Even though some of these findings might be artefacts (e.g., diversification slowdowns intensify with clade size owing to statistical issues or cryptic speciation; Alizon, Kucera, & Jansen, 2008; Machac, Storch, & Wiens, 2013; Moen & Morlon, 2014), it is possible that diversification dynamics vary systematically across phylogenetic scales, such that seemingly contradictory dynamics (e.g., expansion, saturation and decline) might be detected across different segments of the same phylogenetic tree (Figure 1c; Benton & Emerson, 2007; Hedges et al., 2015; Jablonski, 2007; Jetz et al., 2012; Machac, Graham, & Storch, 2018; Morlon et al., 2011). If this is the case, the debate as to whether the dynamics are expansionary or equilibrial should perhaps be reframed in terms of phylogenetic scale. One potentially powerful approach might be to explore the scales over which the different dynamics prevail, identify the ecological factors that determine the shifts between the dynamics, or study how the dynamics combine across nested clades of different ages and sizes to produce the emergent dynamics, observed across an entire phylogeny (see section 3 Phylogenetic scale in practice; Jablonski, 2007; Jetz et al., 2012; Machac et al., 2013, Machac et al., 2018).

Evolutionary disparification varies across the phylogeny as well, because traits (morphological, physiological, behavioural, molecular, etc.) diverge at different rates and, therefore, are conserved over different phylogenetic scales (*sensu* Figure 2d; Blomberg, Garland, & Ives, 2003; Harmon et al., 2010). Even though the rates of trait (or niche) evolution have been the subject of much research, clear generalizations about how they vary across phylogenetic scales have not yet emerged. In some cases, physiological traits, which largely determine species distributions (e.g., frost tolerance; Donoghue, 2008), are conserved at large phylogenetic scales (e.g., at the family level), whereas habitat- and diet-related traits, which mediate species coexistence locally, are phylogenetically labile and conserved only at small scales (Blomberg et al., 2003). However, the opposite pattern has also been observed, where physiological tolerances were conserved at small scales, whereas habitat, diet, body size and feeding method remained unchanged for most of a clade's history (Price et al., 2014). Functional genomics reveal that the phylogenetic scale of trait conservatism might reflect the complexity of the trait (Martiny, Treseder, & Pusch, 2013). In microorganisms, at least, complex traits encoded by many genes (e.g., photosynthesis, methanogenesis) tend to be conserved deep in the phylogenetic tree, whereas simple traits (e.g., the ability to use simple substrates, such as raffinose, citrate or serine) are often phylogenetically labile (Martiny et al., 2013). Future research in genomics might therefore illuminate the interplay of molecular, ecological and evolutionary mechanisms that together determine the phylogenetic scale of conservatism in different types of traits.

2.2 | Community ecology

Community ecology stands out as a field where the effects of phylogenetic scale have been studied extensively, thus illustrating the theoretical and empirical potential of the concept (Cavender-Bares et al., 2009; Münkemüller et al., 2014). Specifically, research across phylogenetic grains and extents has been used to disentangle the different processes that together shape community structure.

To study the phylogenetic structure of a community, researchers often calculate standardized metrics, which can be classified with respect to the phylogenetic grain that they capture (Mazel, Davies, Gallien et al., 2016; Swenson, 2009, 2011; Webb, Ackerly, McPeek, & Donoghue, 2002). The nearest taxon index (NTI), for example, targets the shallow parts of the phylogeny or small phylogenetic grains, as it measures distances between closely related species within a community. The net relatedness index (NRI), in contrast, measures the distances between all species within a community, thus covering an inclusive range of grains, both small and large (Swenson, 2009; Webb et al., 2002). The same sensitivity to community structure at different phylogenetic grains holds for many beta-diversity metrics (e.g., PhyloSor, UniFrac and D_{nn} capture the shallow parts of the phylogeny; Swenson, 2011). Combining metrics capturing different grains, Mazel, Davies, Gallien et al. (2016) found evidence suggestive of recent diversification events in South America (phylogenetic clustering near the tips) but not in Africa (clustering near the root), suggesting that the faunas were assembled differently across the two continents. Parmentier et al. (2014) investigated the structure of tree communities across a range of phylogenetic and spatial grains and concluded that environmental filtering shaped the communities at all but the smallest grains, where competition appeared to predominate.

Phylogenetic extent, too, can have significant effects on phylogenetic metrics of community structure. These metrics are often standardized with respect to null expectations, typically based on a species pool defined by the phylogenetic extent of the group under investigation (Cavender-Bares et al., 2009; Chalmandrier et al., 2013; Parra, McGuire, & Graham, 2010). Changing the phylogenetic extent of their analysis, Parra et al. (2010) obtained different patterns of community structure for hummingbirds (Trochilidae) and their separate subclades (emeralds, mangoes and brilliants). Chalmandrier et al. (2013) manipulated phylogenetic extent through randomization (within clades and between clades) to uncover the effects of biotic interactions, which were masked by environmental filtering at large phylogenetic extents.

Phylogenetic scale might further inform the ecology of microbial communities, community invasions and conservation. Microbial communities, such as those of gut symbionts, are shaped by horizontal

(colonization of the host species) as well as vertical transfer (co-speciation with the host species). Recent work has shown that diet-related (horizontal) colonization predicts the structure of microbial communities at large phylogenetic grains, whereas small-grain community structure reflects mostly the (vertical) co-speciation with the host (Groussin et al., 2017). Moreover, Darwin's naturalization hypothesis postulates that communities are more likely to be invaded by species unrelated to the resident species (reviewed by Thuiller et al., 2010). The potential shift in the phylogenetic scale of the community (measured in terms of the pairwise phylogenetic distance between the constituent species, the age of their most recent common ancestor, etc.) might therefore help to predict the success of potential invaders from different clades (Godoy, Kraft, & Levine, 2014; Thuiller et al., 2010). Finally, phylogenetic metrics that target different depths of the phylogeny might be used to guide conservation priorities (Redding, Mazel, & Mooers, 2014). Some communities consist of closely related species that show a high degree of phylogenetic and functional redundancy (e.g., mammals of South America), whereas others include a variety of species with unique evolutionary histories (e.g., mammals of Africa; Oliveira et al., 2016), which might qualify these communities to receive heightened attention from conservation biologists (Redding et al., 2014).

There are several promising avenues for further integration of phylogenetic scale into community ecology. First, even though cross-grain and cross-extent approaches can be informative, as illustrated by the case studies above (Chalmandrier et al., 2013; Mazel, Davies, Gallien et al., 2016; Parmentier et al., 2014; Parra et al., 2010; Swenson, 2009), phylogenetic grain and extent might prove hard to manipulate separately, as changes in one often produce changes in the other (e.g., an increase in phylogenetic extent also increases the range of grains captured by NRI and NTI; Swenson, 2009; Webb et al., 2002). Therefore, it might be informative to identify the circumstances under which cross-grain approaches (e.g., manipulating the metrics) are more powerful than cross-extent approaches (e.g., manipulating the null model), and vice versa. Second, experiments can be designed to target specific phylogenetic scales, where the processes of competition and environmental filtering have been inferred to operate (Godoy et al., 2014). Third, the grain of the analysis might be extended to include within-species processes, relevant to community structure (e.g., trait variation, demographic structure), as advocated by the field of community genetics (Hersch-Green, Turley, & Johnson, 2011).

2.3 | Biogeography and niche conservatism

Biogeographical patterns, such as species distributions and diversity gradients, might be shaped by the conservatism of ecological niches (Wiens & Graham, 2005), and much discussion has been dedicated to the question of whether or not niches are conserved (Pyron, Costa, Patten, & Burbrink, 2015; Wiens & Graham, 2005). Nonetheless, it might be more fruitful to reframe this question in terms of phylogenetic scale. Niches might be conserved over some phylogenetic scales but not others, and we can investigate how this scale dependence of niche conservatism contributes to various biogeographical patterns.

One such pattern involves regional differences in species richness. Most taxa reach their highest richness in the tropics, but some taxa do not, probably because the climatic niches of these taxa have been conserved over different phylogenetic scales (Buckley et al., 2010; Donoghue, 2008; Wiens & Graham, 2005). For example, most clades of mammals failed to invade the temperate zone, presumably because their climatic niches were conserved over large phylogenetic scales, and consequently accumulated high richness in the tropics. In contrast, relaxed conservatism, restricted to small scales, in the ancestors of present-day rabbits and hares might have allowed the clade to invade the temperate zone (North America and Eurasia) where rabbits and hares later successfully diversified (Rolland, Condamine, Jiguet, & Morlon, 2014). Climatic-niche shifts, which often span a short period in the history of a clade, might lead to diversification episodes that enrich the diversity of regional biotas (Buckley et al., 2010; Donoghue, 2008; Glor, 2010; Wiens & Graham, 2005). Consequently, the evaluation of niche conservatism across phylogenetic scales might inform us about the formation of diversity gradients.

Diversity patterns may be influenced further by regional extinctions (Cahill et al., 2012; Jackson & Weng, 1999), which may be more prevalent at particular phylogenetic scales. Extinctions triggered by climatic changes during the Pleistocene wiped out many genera of trees, but only a few of the tree families (Jackson & Weng, 1999), probably because the climatic niches of the trees were more frequently conserved at the genus level than at the family level (Cahill et al., 2012; Donoghue, 2008). The extinction footprint of climate change might therefore depend on the phylogenetic scale of niche conservatism. Evaluating scale-dependent vulnerability to extinction seems particularly relevant in the face of the ongoing climatic and land-use changes, and the results of such an evaluation might inform us about the patterns of loss of phylogenetic diversity (Purvis, 2008). Taken together, even though it has long been recognized that niches are conserved to varying degrees (Blomberg et al., 2003; Buckley et al., 2010; Donoghue, 2008; Price et al., 2014; Pyron et al., 2015; Wiens & Graham, 2005), few studies have systematically investigated this variation across phylogenic scales despite the promise that such investigation might enhance our understanding of the most conspicuous patterns in biogeography, such as diversity gradients.

2.4 | Macroecology

Macroecologists are concerned with statistical patterns observed across large spatial and temporal scales, such as body size distributions, species–area relationships or species-abundance distributions (Brown, 1995). They rarely consider phylogenetic scale explicitly in their research even though the concept may help to identify 'ecological laws' (universal patterns in ecology; Marquet et al., 2004; Storch & Šizling, 2008) and the mechanisms (biological, statistical and geometric) behind these laws and other non-universal patterns (Marquet et al., 2004; Storch & Šizling, 2008).

Many of the famous patterns in macroecology emerge only across a narrow range of phylogenetic scales (Buckley et al., 2010; Damuth, 1981; Šizling, Kunin, Šizlingová, Reif, & Storch, 2011; Storch & Šizling,

2008). For example, population abundance and body mass are negatively correlated across birds and mammals (which represent large phylogenetic scales), presumably because the low metabolic requirements of small-bodied species permit these species to reach high abundances (Damuth, 1981; Isaac, Storch, & Carbone, 2011; Figure 1b). However, the correlation often disappears in narrowly defined taxa, representing small phylogenetic scales and comprising ecologically similar species (Cotgreave, 1994; Figure 2d), within which small-bodied species are competitively inferior to large-bodied species (*sensu* Figure 1d; Cotgreave, 1994).

Multiscale analyses may also be used to test the so-called 'ecological laws'. By definition, these laws must be universal and therefore hold across phylogenetic scales (*sensu* Figure 2d). Two classic examples of such laws, the SAR and SAD, were presumed to conform universally to particular mathematical forms (the power-law function and the lognormal distribution, respectively; Preston, 1948; Rosenzweig, 1995). However, if two sister taxa follow power-law SARs and lognormal SADs that differ in their parameters, it can be demonstrated mathematically that the clade containing both sister taxa cannot follow either the power-law SAR or the lognormal SAD (Šizling et al., 2011; Storch & Šizling, 2008). The fact that these patterns, consequently, cannot be truly universal means that they do not represent ecological laws, as was previously presumed, and implies either that current theories to explain these patterns are fundamentally ill founded or that the patterns pertain to certain phylogenetic scales only (Storch & Šizling, 2008). The latter possibility suggests that phylogenetic scales form domains (Box 2), within which some of the current theories might apply, and an explicit delimitation of these domains might consequently further inform the theories.

3 | PHYLOGENETIC SCALE IN PRACTICE

In this section, we consider strategies to investigate patterns across phylogenetic scales. Phylogenetic scale often has been considered within an exploratory framework, whereby patterns were identified across a range of scales and then explained in the light of specific events or mechanisms. Another possible approach relies on testing a priori hypotheses, which are based on mechanisms assumed to operate over certain phylogenetic scales. Both of these approaches (exploratory and hypothesis testing) have their strengths, and either may be appropriate, depending on the objective of a given study. Either approach can be pursued using existing methods (Tables 1 and 2) to investigate a variety of attributes (diversification rates, the strength of niche conservatism, patterns of community structure, etc.) across scales. The attributes may vary without any obvious trend (phylogenetic scale dependence) or with a trend across the phylogeny (phylogenetic scaling) or stay unchanged across discrete segments of the phylogeny (phylogenetic domains; Box 2).

3.1 | Choice of phylogenetic scale

Most researchers are aware that the choice of the studied clade implicitly determines the phylogenetic scale of their investigation. Nonetheless, studies are rarely designed around the phylogenetic scale most suitable for a particular question, instead they are often designed around a clade of interest (especially around named taxa, such as angiosperms, prokaryotes, birds, tetrapods or vertebrates). The implicit choice of the phylogenetic scale might then largely predetermine our conclusions. For example, to address the question whether competition limits species coexistence, small phylogenetic extents (e.g., genera, or clades where species can be reasonably assumed to compete with each other) produce more meaningful tests than large extents (e.g., birds, tetrapods), where most species are so ecologically divergent that competition is unlikely to be detected (Cavender-Bares et al., 2009; Münkemüller et al., 2014). The same applies to the investigation of niche conservatism, diversification slowdowns or macroecological patterns (e.g., universal patterns are more likely to emerge at large extents where clade-specific idiosyncrasies cancel out; O'Meara, 2012; Šizling et al., 2011; Storch, 2016). Nonetheless, even with a specific question at hand, it might sometimes be preferable to avoid working at a single scale and, instead, investigate how the attribute of interest behaves at multiple scales.

3.2 | Phylogenetic scale dependence

Many attributes naturally vary, without any clear trend, across the phylogeny, especially when the phylogeny is large ($\geq$1,000 species; Figure 1 and Box 2; O'Meara, 2012), such that the conclusions based on one phylogenetic scale might not hold for another scale. Cetacean systematists, for example, had long been perplexed as to why there is little correspondence between diversification dynamics estimated from the fossil record and phylogenetic trees (Morlon et al., 2011). The correspondence between the two datasets emerged only when considering diversification heterogeneity across clades. The results suggested that individual clades, representing small phylogenetic extents (i.e., rorquals, ocean dolphins, porpoises and beaked whales), had their own diversification dynamics that were obscured at the phylogenetic extent of cetaceans as a whole (Morlon et al., 2011), implying that the conclusions from one scale did not apply to another scale. Moreover, when detected, phylogenetic scale dependence reveals the natural variation in the attribute of interest that would otherwise remain hidden.

3.3 | Phylogenetic scaling

Phylogenetic scaling refers to the situation when the attribute of interest changes following a clear trend along the scale axis (e.g., the strength of niche conservatism systematically decreases with clade age; Box 2). Scaling should be most prevalent across mutually nested clades because the patterns associated with large clades are inherently determined by the patterns of clades nested within them. For example, the diversification rate of a clade is determined by the rate values of its subclades, similar to the way in which the species richness of a spatial plot is determined by the richness of its subplots. Consequently, it should be possible to predict the value of an attribute at a particular phylogenetic scale from the knowledge of those values at other scales, much as it is possible to estimate species richness within large geographical areas, based on the knowledge of richness within small areas (Chave, 2013; Storch, 2016). When characterized mathematically,

TABLE 1 Ecological and evolutionary attributes that can vary across phylogenetic scales

Field	Examined attribute	Methods for the evaluation of the attribute	Implementation in R
Evolution and diversification	Diversification mode	Coalescent inference to distinguish between accelerations, slowdowns and saturation (Morlon, Potts, & Plotkin, 2010)	RPANDA (Morlon et al., 2016)
	Diversification rate	Product–moment estimators (Magallon & Sanderson, 2001), equal-splits measures (Jetz et al., 2012)	ape (Paradis, Claude, & Strimmer, 2004), geiger2 (Pennell et al., 2014)
	Slowdown strength	Gamma statistic (Pybus & Harvey, 2000)	laser (Rabosky, 2007)
Community ecology and biogeography	Community structure and phylogenetic diversity	Phylometrics (NRI, NTI, MNND, MPD, PD) (Faith, 1992; Swenson, 2009; Webb et al., 2002)	picante (Kembel et al., 2010), PhyloMeasures (Tsirogiannis & Sandel, 2016)
Niche conservatism and trait evolution	Phylogenetic signal	Pagel's lambda (Freckleton et al., 2002), Blomberg's K (Blomberg et al., 2003; but see Revell, Harmon, & Collar, 2008)	geiger2 (Pennell et al., 2014), picante (Kembel et al., 2010)
	Evolutionary rates	Brownian motion model (Edwards & Cavalli-Sforza, 1964; Felsenstein, 1985), Ornstein–Uhlebeck model (Hansen, 1997), ACDC model (Blomberg et al., 2003)	ape (Paradis et al., 2004), geiger2 (Pennell et al., 2014)
Biogeography and macroecology	Statistical relationship	Function relating two variables (linear, polynomial, exponential) or distribution functions (lognormal, exponential)	base (R Core Team, 2017), nlme (Pinheiro, Bates, DebRoy, Sarkar, & R Core Team, 2016)
	Relationship strength	Pearson's correlation, Spearman's correlation	base (R Core Team, 2017)

Note. Each attribute is listed together with concrete examples of methods for its evaluation. These methods return the results for one clade at a time and therefore need to be repeated across clades covering different scales to investigate phylogenetic scale dependence, scaling and the domains of scale (Box 2).

phylogenetic scaling should allow for predictions across phylogenetic scales not covered by the phylogeny under consideration (i.e., upscaling or downscaling).

3.4 | Domains of phylogenetic scale

Domains are discrete segments of a phylogeny, such as monophyletic clades or sets of nodes, which show homogeneity in the attribute of interest (Box 2). Traditionally, phylogenetic domains were delimited by taxonomists whose objective was to organize species into biologically meaningful units, such as families, orders or classes. These units are based mostly on morphological and ecological attributes. Phylogenetic domains, however, can also encompass clades that show diversification homogeneity, comparable rates of morphological evolution or similar life-history trade-offs. Therefore, the delimitation of domains might rely on the natural history of the group (key innovations, episodes of historical dispersal, extinction events, etc.) but also on statistical methods that do not require any such prior knowledge (Table 2). The statistically delimited domains might be more transparent and reproducible, but harder to interpret biologically. However, they may also reveal otherwise unnoticed events and shifts in a clade's history that may have contributed significantly to its present-day characteristics.

Phylogenetic domains may also facilitate statistical inference, given that most comparative methods assume that the attributes analysed

TABLE 2 Methods that work across phylogenetic scales

Studied pattern/process	Method	Results	Software and references
Diversification	BAMM, MEDUSA, REVBAYES	Shifts in diversification rates and regimes (constant diversification, accelerations, slowdowns) across the entire phylogeny	BAMMtools (Rabosky, 2014), geiger2 (Alfaro et al., 2009; Pennell et al., 2014), REVBAYES (Höhna et al., 2016)
Trait evolution	BAMM, SURFACE, NODIV, MOTMOT, PIC, OU, ACDC, BM, CONSENTRAIT	Changes in the values and rates of traits (morphological, behavioural, physiological, molecular) across the phylogeny	BAMMtools (Rabosky, 2014), surface (Ingram & Mahler, 2013), nodiv (Borregaard et al., 2014), MOTMOT (Thomas & Freckleton, 2012), ape and geiger2 (Blomberg et al., 2003; Butler & King, 2004; Edwards & Cavalli-Sforza, 1964; Felsenstein, 1985; Hansen, 1997; Paradis et al., 2004; Pennell et al., 2014), consenTRAIT (Martiny et al., 2013)
Geographical distributions	BIOGEOBEARS, LAGRANGE, NODIV, DIVA, BDTT	Dispersal and colonization events, shifts in the geographical distributions, changes in community structure	BioGeoBEARS (Matzke, 2014), LAGRANGE (Ree et al., 2008), nodiv (Borregaard et al., 2014), DIVA (Ronquist & Sanmartín, 2011), BDTT (Groussin et al., 2017)

Note. These methods return comprehensive results for the entire phylogeny, which can be used to investigate scale dependence, scaling and the domains of scale (Box 2). The results of each method are briefly explained, and relevant sources for further reference are listed.

Box 2. Research across phylogenetic scales

Many attributes, including diversification rates, the strength of niche conservatism or the phylogenetic structure of a community, vary across phylogenetic scales (Table 1). They can vary in three different ways:

a. **Phylogenetic scale dependence** refers to the situation when the attribute of interest changes across phylogenetic scales without any clear trend. In this case, the results from one scale might be difficult to extrapolate to another scale (e.g., the rate of trait evolution changes unpredictably with the size of the clade).

b. **Phylogenetic scaling** occurs when the attribute of interest changes systematically along the scale axis. The interpretation of scaling is at least threefold, depending on the underlying mechanism (note that only one of the mechanisms is biological):

   1. **Statistical scaling** is a sample-size effect whereby the statistical power of the analysis increases with increasing scale, such that the attribute of interest appears to change systematically from small to large scales. For example, diversification slowdowns tend to strengthen with clade size, partly because a slowdown is easier to detect in a large clade (Machac et al., 2013). Although the inferred values of the attribute itself may be technically correct, their systematic variation across scales is biologically irrelevant.
   2. **Artefacts** result when a statistical analysis becomes increasingly misleading toward the deep nodes of the phylogeny, resulting in incorrect and potentially biased estimates for the attribute of interest (e.g., ancestral reconstructions under dispersal–vicariance models often erroneously suggest that the ancestor occupied all of the regions examined; Ronquist & Sanmartín, 2011). Methodological artefacts can be mitigated using various statistical corrections or when the results are validated using supplementary data, such as fossils.
   3. **Phylogenetic scaling in the strict sense** occurs when the studied attribute changes across scales because the underlying biological process changes. This type of scaling can therefore inform us about the processes that generate the observed patterns. When described mathematically, true scaling may allow extrapolation across scales, even those not included in the original study (i.e., downscaling or upscaling of the patterns under study).

c. **Domains of phylogenetic scale** refer to the segments of the phylogeny (monophyletic clades, sets of nodes, etc.) within which the attribute of interest stays relatively unchanged. The attribute might change abruptly between domains, indicating changes in the underlying biological processes. For example, a shift in the diversification regime detected on a phylogeny might indicate a change in the life-history trade-offs, the emergence of a key innovation, etc.

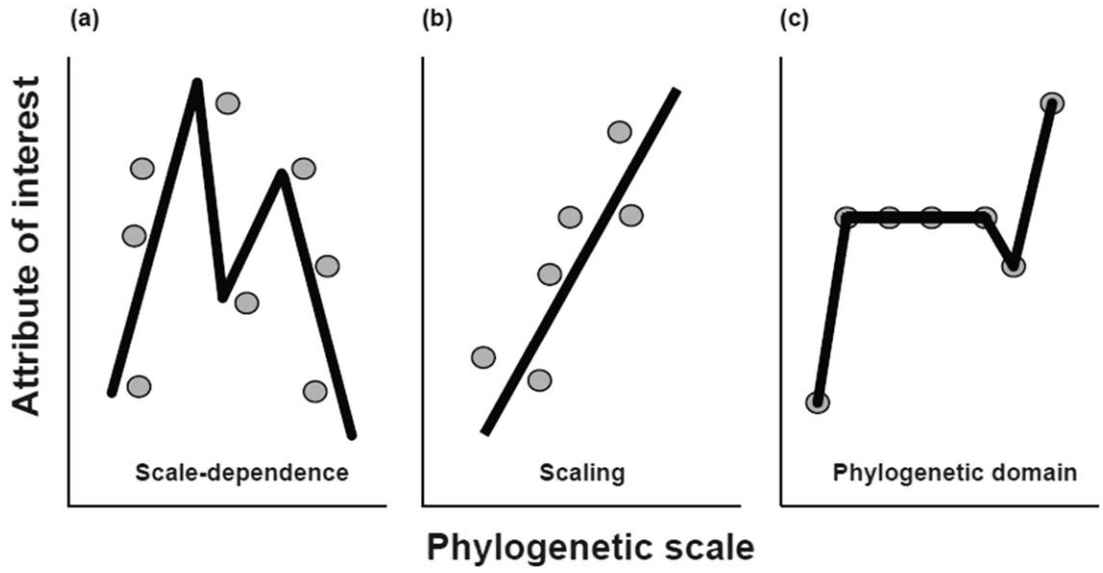

FIGURE. Numerous attributes can be studied across phylogenetic scales (Tables 1 and 2), which can be defined in terms of clade size, clade age, tree depth (i.e., time slices through the tree), etc. The data points in all three panels represent clades for which the attribute (e.g., diversification rate) and the phylogenetic scale (e.g., clade age) were calculated. The right panel depicts only one phylogenetic domain, delimited by the horizontal segment, within which the examined attribute stays unchanged.

are homogeneous (e.g., regression slopes do not vary across genera within the analysed family, diversification is homogeneous across the analysed phylogenetic lineages) and return spurious results when applied to clades that show a mixture of patterns and processes (Maddison & FitzJohn, 2015; Mazel, Davies, Georges et al., 2016; Morlon et al., 2011; O'Meara, 2012; Figure 1d). Phylogenetic domains may therefore help to identify when comparative methods report reasonably reliable results and when their conclusions must be interpreted with caution because the results span different domains and the underlying assumptions have been violated.

3.5 | Methods of cross-scale analysis

Methods that can be used to investigate patterns across phylogenetic scales either evaluate the attribute of interest for one clade at a time (Table 1) or work across the entire phylogeny and return tree-wide results that can be investigated further specifically with respect to phylogenetic scale (Table 2). The method introduced by Borregaard et al. (2014), for example, proceeds across the phylogeny and identifies the nodes whose descendant clades underwent conspicuous geographical, phenotypic or ecological shifts (Borregaard et al., 2014). Similar methods have also been developed to investigate community structure across various phylogenetic grains (Parmentier et al., 2014) and phylogenetic extents (Chalmandrier et al., 2013). In macroevolution, statistical algorithms that proceed across the entire phylogeny are not uncommon and have been used to identify shifts in diversification rates (e.g., BAMM, MEDUSA, REVBAYES; Alfaro et al., 2009; Höhna et al., 2016; Rabosky, 2014) and historical distributions (e.g., LAGRANGE, BIOGEOBEARS; Matzke, 2014; Ree, Smith, & Baker, 2008; Ronquist & Sanmartín, 2011). These shifts then delimit those segments of the phylogeny that are homogeneous in terms of their diversification and/or geographical distributions, such that the segments might be used as phylogenetic grains for further analysis (i.e., elementary and homogeneous units of analysis) or interpreted as phylogenetic domains (Box 2). Phylogenetically independent contrasts (PICs; Felsenstein, 1985) are also calculated for the entire phylogeny and thus capture trends across an inclusive range of phylogenetic scales. Yet, they are rarely explored with respect to the phylogenetic scale itself (*sensu* Figure 2d), although such an approach was advocated early on in the history of the development of these methods (Garland, Harvey, & Ives, 1992; e.g., contrasts might decline from the root toward the tips, indicating progressively decreasing evolvability in the trait of interest). Transformations that distort the relative lengths of branches within a tree (e.g., the rho transformation) have also been advocated as an efficient way of comparing evidence from different (especially shallow and deep) parts of the tree (Grafen, 1989). These examples together illustrate the range of tools that can readily be used for cross-scale analyses. Most studies, however, work with select clades only, despite the commonly cited concern that clade selection is typically non-random and might bias the results of the study (Cusimano & Renner, 2010), whereas cross-scale analyses remain relatively underused.

Two potential issues, associated with the evaluation of all nodes within a phylogeny, are data non-independence and nestedness. Non-independence can readily be accommodated by widely used comparative methods (e.g., PIC, PGLS; Felsenstein, 1985; Freckleton, Harvey, & Pagel, 2002; Grafen, 1989). These methods typically estimate the same parameters as their conventional counterparts (e.g., intercepts, regression slopes, group means) but adjust the confidence intervals of these parameters based on the inferred degree of phylogenetic correlation in the data (Freckleton et al., 2002; Rohlf, 2006). The nestedness of the data is more difficult to accommodate. For example, the diversification rate of a clade is inherently determined by the rate values across its constituent subclades. Nestedness therefore extends beyond the phylogenetic correlation of rate values and reflects how the value for a clade is produced by the subclade values. This information cannot readily be accommodated with the currently available methods (Felsenstein, 1985; Freckleton et al., 2002; Grafen, 1989; O'Meara, 2012), which therefore do not guarantee proper estimates of statistical significance across nested data. For these reasons, we argue that parameter estimates can be extracted, compared and analysed across nested clades, but their significance needs to be interpreted cautiously. Likewise, scaling relationships in spatial ecology (e.g., species–area relationship) can be studied meaningfully without correcting for the nestedness of the measured units (e.g., grid cells, ecoregions, biomes), given that well-developed theory exists to link the measurements from different scales (Chave, 2013; Storch, 2016). Therefore, new theories that would illuminate how different attributes of interest (e.g., diversification rates, regression slopes, phylogenetic signal) combine and compound across nested hierarchies, as well as methods that would reliably capture these changes, would surely enrich the investigation of patterns across the phylogeny.

4 | CONCLUSION

It is well established that different processes dominate over different spatial and temporal scales. Phylogenetic scale has received only limited attention even though much research in ecology and evolution today relies on molecular phylogenies (Tables 1 and 2). Explicit consideration of different aspects of phylogenetic scale, including grain, extent, scale dependence, phylogenetic scaling and the domains of phylogenetic scale can therefore inform multiple fields (e.g., macroevolution, community ecology, biogeography, macroecology).

We discussed phylogenetic scale largely in isolation from spatial and temporal scales, but these types of scale will often be related. For instance, competitive exclusion may be prominent among closely related species within local communities over short time periods (Cavender-Bares et al., 2009). Conversely, plate tectonics might influence deeper nodes in a phylogeny and operate over broad geographical extents (Willis & Whittaker, 2002). In some notable cases, however, the spatial and phylogenetic scales may not be related. Diversity anomalies, such as New Caledonia or Madagascar, represent examples of decoupling where rich biotas that encompass extensive phylogenetic scales diversified in a relatively small region (Espeland & Murienne, 2011). In contrast, recent radiations within grasses and rodents have had a large geographical footprint but encompass only a few relatively

young clades (Edwards et al., 2010). Evaluating when different types of scale are coupled (or decoupled) might yield new insights into the evolutionary history of different clades and regions (Levin, 1992; Rosenzweig, 1995; Wiens, 1989; Willis & Whittaker, 2002).

We hope that the perspective presented here will spur further theoretical, empirical and methodological research. Explicit consideration of phylogenetic scale may turn our focus away from particular mechanisms toward the appreciation of the interplay of multiple processes that together, but over different phylogenetic scales, shape the diversity of life.

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